ON THE SIZE VARIATION OF *CLAUSILIA BIDENTATA* AND *ENA OBSCURA* WITHIN A "LOCALITY".

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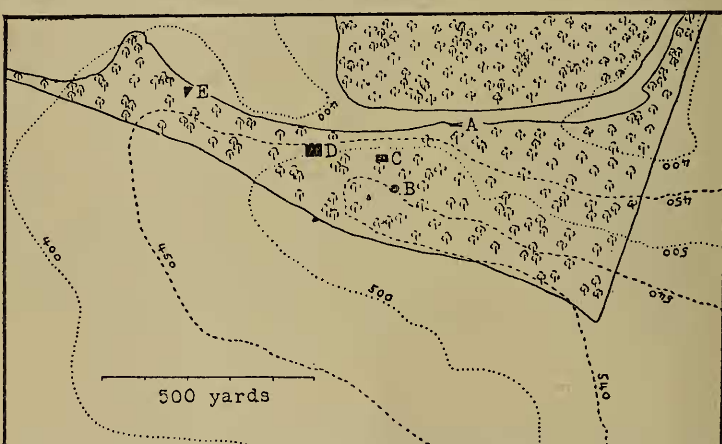
§ 1. It was shown in a previous communication [1] that specimens of *Clausilia bidentata* from similar habitats in the same neighbourhood could generally be readily distinguished from one another by differences in size. It was there shown that the snails living on one stone wall were usually larger or smaller than those living on a similar stone wall half a mile away, and therefore did not belong to precisely the same familial group. A question which was not then examined was how near together, in a habitat roughly homogeneous in character, such distinguishable loci might be—a locus for any species being an area throughout which that species is uniform in character. Facilities, imperfect but tolerable, for collecting over an extended period in a Wiltshire beech-wood, gave an opportunity for making some further inquiries into these questions.



Tower Hill Plantation.

§ 2. Tower Hill Plantation lies on a ridge of high chalk land, two miles west of Boscombe, in south-east Wilts. It forms part of a great ring plantation, and in its present form is presumably modern, though the northern slope is too steep to have ever allowed cultivation.[2] In the parts with which we are concerned it is a typical close-canopied beech-wood ; there is no ground flora except

[1] Journ. of Conch., vol. xvi, 1919, p. 10.

[2] I could find no signs of *Ena montana*, *Limax cinereo-niger*, or *L. tenellus* which would have indicated an ancient wood ; even *Helicigona lapicida* was absent, though it occurs a mile away in another wood.

for some moss in a few places and a scattered growth of *Cephalanthera* generally. The tree-trunks are also, with rare exceptions, free from moss or any but a scanty growth of lichens. The wood runs roughly east and west (see sketch-map); its southern edge nearly corresponds with the highest part of the ridge, while its northern part lies on a steep slope leading to a narrow valley, with a second wood beyond. The prevailing winds being from the south-west, the upper parts of the wood are exposed, while the northern slope and the valley beneath are much more sheltered. In a general way the whole wood would usually be considered a single homogeneous locus, and specimens collected in one part would not be separated from those from another part.

§ 3. The present inquiry was made to test this presumption by finding out whether *Clausilia bidentata* from one part of the wood was larger or smaller than from another part; incidentally, *Ena obscura* was also examined less fully.

To this end collections were made in five different areas (see map, p. 34), as follows:—

A: Six trees in a line 26 yards long in the valley, and very sheltered.

B: Thirteen trees in a rough circle of about 23 yards, 200 yards south-west of A, and some 120 feet higher, nearly on the top of the hill.

C: Twenty-one trees in 27 by 15 yards, 50 yards north and west of B, a little lower and more sheltered behind the hill-top; some moss on ground and trees.

D: Twenty-two trees in 41 by 30 yards, 120 yards west of *C*; lying on a steep slope, the difference in level between top and bottom being about 40 feet.

E: Twenty trees in a triangle of about 25 yards, 320 yards west of D; low and sheltered.

The shading varied to some extent; A was the lightest area, with thin trees to the south and none to the north. C and D are both open to some extent owing to the steep slope to the north. At B the trees are rather thin to the south, close on the other sides. E is the darkest locus. In three of these areas collections were made from individual trees as well as from the area as a whole, i.e. from six trees in area A, from three in area B, and from six in area D: their relative positions are shown in diagram 1. On an average there is one tree to about 35 or 40 square yards of ground.

The snails were collected as opportunity offered on various occasions between June 19 and December 2, 1918, as they crawled or sat upon the trunks, all the specimens found on the selected trees being taken without selection. The measurements and computations were made as already described.[1] A certain number of shells had to be excluded from measurement on account of decollation, in all

[1] Journal of Conch., vol. xvi, 1919, p. 11.

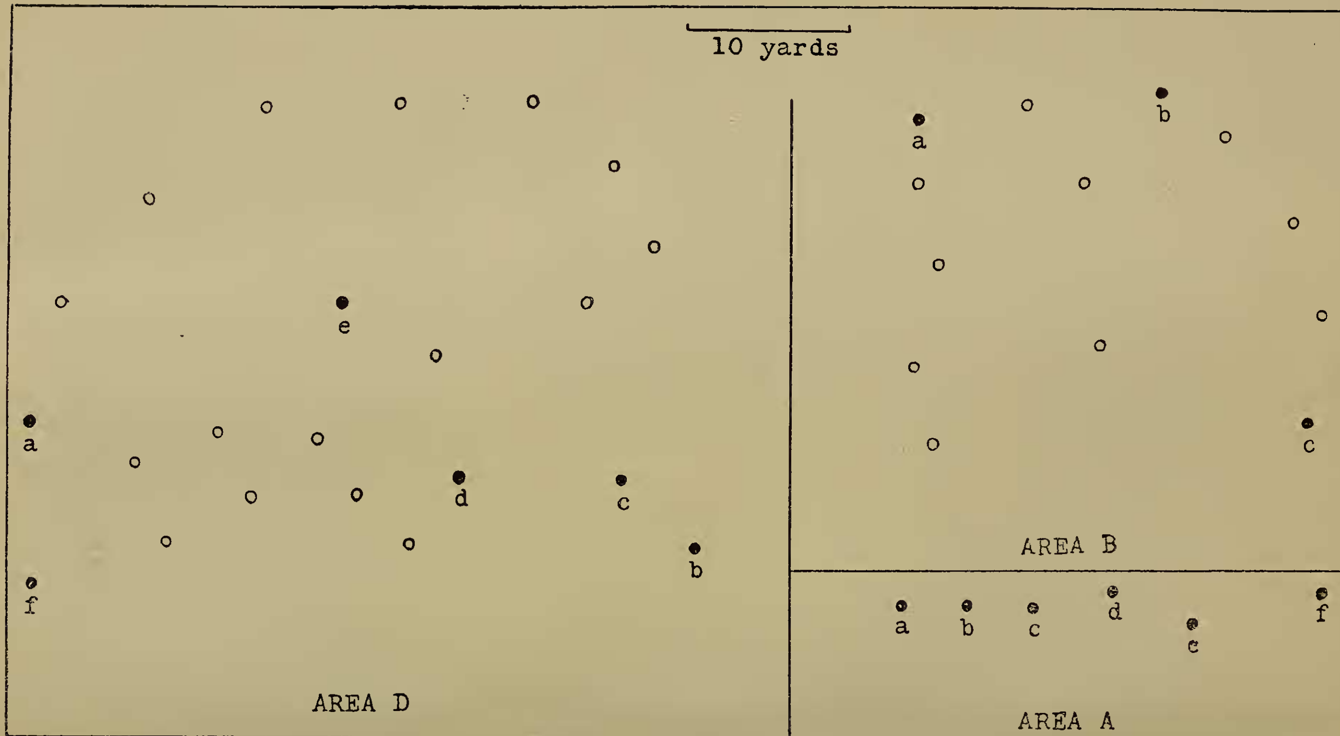

10 yards
a
b
c
d
e
f
AREA D
a
b
c
AREA B
a
b
c
d
e
f
AREA A

Table 1.—Showing the Altitudes and Diameters of *Clausilia bidentata* from Fifteen Trees in Three Areas.

Altitude.

Tree.	Number of specimens.	8.	8·5.	9.	9·5	10.	10·5.	11	11·5.	12.	12·5.	Minimum.	Maximum.	Mean.	Standard deviation.	Coefficient of variation.
Aa	41		1	1	15	16	4	3			1	8·9	12·5	10·139	0·646	6·4
b	30		1	8	9	7	3	1	1			8·9	11·6	9·866	0·662	6·7
c	59			3	15	15	18	8				9·2	11·3	10·310	0·561	5·5
d	72			4	24	21	18	4	1			9·0	11·4	10·179	0·536	5·3
e	80			9	19	30	15	7				9·1	11·4	10·150	0·551	5·4
f	128	1	3	16	34	35	31	7	1			8·4	11·8	10·085	0·624	6·2
Ba	204	1	12	52	69	49	20	1				8·4	11·2	9·732	0·550	5·6
b	83		8	15	27	23	9	1				8·7	11·2	9·778	0·584	6·0
c	113	1	6	21	37	33	12	3				8·4	11·4	9·833	0·583	5·9
Dd	234	2	16	55	97	45	16	3				8·3	11·2	9·685	0·540	5·5
b	164	2	17	44	58	30	11	1	1			8·4	11·7	9·624	0·585	6·1
c	186	2	16	48	70	38	10	1	1			8·0	11·7	9·644	0·556	5·8
d	160	1	16	44	56	27	12	4				8·3	11·4	9·650	0·594	6·1
e	115	1	16	21	34	25	15	2		1		8·4	12·1	9·743	0·692	7·1
f	121	4	18	29	35	22	11	1	1			8·1	11·8	9·593	0·678	7·1

Diameter.

Tree.	2·2.	2·3.	2·4.	2·5.	2·6.	2·7.	2·8.	2·9.	Mean.	Standard deviation.	Coefficient of variation.
Aa			4	15	16	4	2		2·563	0·096	3·7
b		1	3	4	15	6	1		2·583	0·107	4·1
c			2	12	29	10	6		2·610	0·095	3·6
d		2	6	20	29	12	3		2·572	0·106	4·1
e		1	2	17	33	20	7		2·617	0·100	3·8
f		1	8	27	54	29	7	2	2·602	0·106	4·1
Ba		4	20	73	80	24	3		2·554	0·094	3·7
b		1	12	28	31	10	1		2·548	0·096	3·8
c			14	40	43	12	3	1	2·558	0·104	4·1
Dd	1	3	23	74	92	39	2		2·562	0·097	3·8
b		3	22	71	54	13	1		2·534	0·089	3·5
c		2	24	72	59	25	3	1	2·551	0·100	3·9
d		4	32	45	59	18	2		2·538	0·104	4·1
e		4	15	43	33	19	1		2·544	0·105	4·1
f		9	19	38	43	10	2		2·526	0·110	4·3

39 out of 2,994, or 1·3 per cent. There is no evidence that large or small individuals are more likely to lose their apical whorls than those of moderate size, and the error introduced in this way may be neglected.

§ 4. With respect to the first question, whether shells from individual trees close to one another show differences in size, there are data for six trees in area A, three trees in area B, and six trees in area D. The figures for these fifteen lots are given in table I, and the result of the appropriate calculations in table II. From these it appears that the shells from closely adjacent trees are demonstrably different in size in two instances only, Ab being definitely shorter than Ac, and Da broader than Df. With six trees in area A there are fifteen comparisons and fifteen possible differences, in area B three, in area D fifteen, in all thirty-three, or, if we take altitudes and diameter separately, sixty-six. Of these two only are present. This negative result throws no light on the question as to how far a familial assembly of *Cl. bidentata* ranges; it might mean that the range is greater than the area served by a single tree, or that families living near one another are not distinguishable in size with the available data.

Table II. — SHOWING THE SIGNIFICANT DIFFERENCE IN ALTITUDE (+) AND DIAMETER (o) FOR FIFTEEN SEPARATE TREES IN THREE AREAS.

	Aa	*Ab*	*Ac*	*Ad*	*Ae*	*Af*	*Ba*	*Bb*	*Bc*	*Da*	*Db*	*Dc*	*Dd*	*De*	*Df*
Aa							+		+	+	+	+	+	+	+
Ab			+												
Ac		+					+o	+o	+o	+o	+o	+o	+o	+o	+o
Ad							+	+	+	+	+	+	+o	+	+
Ae							+o	+o	+o	+o	+o	+o	+o	+o	+o
Af							+o	+o	+o	+o	+o	+o	+o	+o	+o
Ba	+		+o	+	+o	+o									
Bb			+o	+	+o	+o									
Bc	+		+o	+	+o	+o									
Da	+		+o	+	+o	+o									o
Db	+		+o	+	+o	+o									
Dc	+		+o	+	+o	+o									
Dd	+		+o	+	+o	+o									
De	+		+o	+	+o	+o									
Df	+		+o	+	+o	+o				o					

§ 5. That the shells in the different areas are largely differentiated in size is shown pretty plainly if individual trees in one area are compared with individual trees in another. Taking table II as a whole, there are 105 possible comparisons; eighteen differ in altitude only, one in diameter only, and twenty-seven in both altitude and diameter, forty-six in all. The comparison is, however, best made in the simple form of taking each area as a whole, as in tables III and IV. The shells from each area differ in altitude from those in each of the other areas, with the exception that C and E are not differentiated. Nine of the ten possible differences

Table III.—Showing the Altitudes and Diameters of *Clausilia bidentata* from Five Areas in the same Wood

		Altitude.															Diameter.										
Area.	Number of specimens.	8.	8·5.	9.	9·5.	10.	10·5.	11.	11·5.	12.	12·5.	Minimum.	Maximum.	Mean.	Standard deviation.	Coefficient of variation.	2·2.	2·3.	2·4.	2·5.	2·6.	2·7.	2·8.	2·9.	Mean.	Standard deviation.	Coefficient of variation.
A	410	1	5	41	116	124	89	30	3		1	8·4	12·5	10·134	0·603	6·0		5	25	95	176	81	26	2	2·595	0·104	4·0
B	400	2	26	88	133	105	41	5				8·4	11·4	9·770	0·568	5·8		5	46	141	154	46	7	1	2·554	0·096	3·8
C	744	1	27	122	256	218	94	24	2			8·2	11·8	9·906	0·566	5·7		12	90	256	273	109	4		2·552	0·088	3·4
D	980	12	99	241	350	187	75	12	3	1		8·0	12·1	9·657	0·598	6·2	1	25	135	343	340	124	11	1	2·545	0·101	4·0
E	421		26	58	121	133	64	14	4	1		8·5	12·2	9·954	0·624	6·3		4	37	149	156	59	16		2·563	0·100	3·9

Table V.—Showing the Altitudes and Diameters of *Ena obscura* from the same Five Areas.

Area.	Number of specimens.	7·2.	7·4.	7·6.	7·8.	8·0.	8·2.	8·4.	8·6.	8·8.	9·0.	9·2.	9·4.	9·6.	9·8.	Minimum.	Maximum.	Mean.	Standard deviation.	Coefficient of variation.	3·5.	3·6.	3·7.	3·8.	3·9.	4·0.	Mean.	Standard deviation.	Coefficient of variation.
A	101				2	4	11	11	21	25	14	5	5	2	1	7·8	9·9	8·751	0·393	4·5		24	33	36	8		3·728	0·091	2·4
B	131	1	0	2	7	10	32	28	26	14	9	2				7·2	9·3	8·453	0·348	4·1	3	30	56	31	9	2	3·714	0·098	2·6
C	119	1	1	4	4	12	17	27	21	16	8	5	2	1		7·3	9·6	8·505	0·426	5·0	3	37	50	24	5		3·693	0·088	2·4
D	105	1	0	2	10	24	20	15	20	9	1	3				7·2	9·3	8·338	0·367	4·4	7	42	36	17	2	1	3·670	0·095	2·6
E	110		1	1	2	8	17	16	18	16	22	7	2			7·5	9·4	8·643	0·403	4·7	2	16	60	30	2		3·713	0·074	2·0

exist, and five of the ten possible differences in diameter. Evidently, therefore, a beech-wood such as I am dealing with is not a homogeneous locus *quâ* the size of *Cl. bidentata*. The data for *Ena obscura*, unfortunately with less ample material, given in tables V and VI show that the same differentiation is shown by this species, though to a less degree; seven of the ten possible differences exist in altitude, diameter, or both.

Table IV. — Showing the significant difference in altitude (+) and diameter (o) for the five areas compared with one another, *Cl. bidentata*.

	A	*B*	*C*	*D*	*E*
A		+o	+o	+o	+o
B	+o		+	+	+
C	+o	+		+	
D	+o	+	+		+o
E	+o	+		+o	

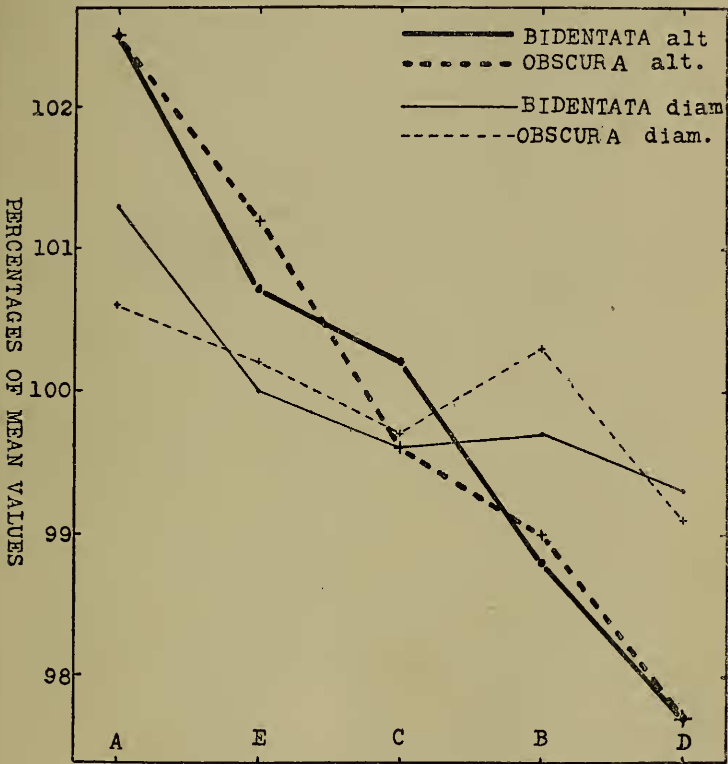
Table VI. — Showing the significant difference in altitude (+) and diameter (o) for the five areas compared with one another, *E. obscura*.

	A	*B*	*C*	*D*	*E*
A		+	+	+o	
B	+			o	+
C	+			+	
D	+o	o	+		+o
E		+		+o	

§ 6. Our beech-wood, then, does not form a locus in the sense that it is similar in all its parts as regards the size of the two snail-shells we have considered. The snails which live in different parts of it clearly differ in size, and on the basis of their differences the wood, which in a general way is homogeneous, may be dissected into many loci. It is an obvious question whether such varieties as these are correlated with variations in external circumstances, or whether they should be regarded as fortuitous results of relative isolation; clearly snails living several hundred yards apart cannot be suspected of much interbreeding. Bateson [1] says very truly that we have in the past been too ready to find the explanation of local differences in the localities rather than in the organisms. The present data may, I think, throw some light on the point. If the local differences arise from mutation within the organisms, the variations in *Clausilia bidentata* should have little or no relation with those in *Ena obscura*; if, on the other hand, they are caused by differences in environmental circumstances it is possible that the variations in the two species would run more or less parallel. Such proves to be the case in the present instance, for if we arrange the loci in descending order we get :—

[1] *Problems of Genetics*, 1913, p. 131.

Altitude.		Diameter.		Volume.[1]	
bidentata.	*obscura.*	*bidentata.*	*obscura.*	*bidentata.*	*obscura.*
A	A	A	A	A	A
E	E	E	B	E	E
C	C	B	E	C	B
B	B	C	C	B	C
D	D	D	D	D	D



It seems hardly credible that such a correspondence of relative sizes in the different loci as is shown in diagram 2 should be of fortuitous internal origin rather than an expression of environmental circumstances. The two species being of similar habits, it is not unlikely that they would be affected in the same way by similar conditions, and as far as their size is concerned such appears to be the case in the five cases under consideration.

[1] Calculated on the (doubtless erroneous) assumption that the measured diameter = the diameter of the base of a cone and the measured altitude its height.

§7. The connexion between the sizes and environments is more obscure. It is suggestive that the largest specimens came from the two most sheltered areas (A and E), while B, the most exposed, yields the second smallest lot; the more so because in the Portmadoc series exposure was associated with small *Clausilia bidentata*. In North Wales, however, the densely shaded and sheltered loci also yielded small specimens—a difference possibly due to the difference in climate, close shelter on the chalk in Wilts giving agreeably damp conditions, which are exaggerated on the less porous strata of Portmadoc with a heavier rainfall to a degree of wetness which is detrimental. "Shelter" and "exposure" may be presumed to affect snails mostly by way of dampness; the duration of moist conditions after rainfall is greatly influenced by ventilation, and in exposed places the time during which snails can move about is considerably curtailed by rapid drying.

§8. It is interesting to note that the local conditions which influence decollation have no relation to those which influence size. Note was taken of the number of decollated shells from each area; they are most [1] frequent in A, least in E. The natural presumption is to look on decollation as an indication of vague unhealthiness, but it is as likely associated with exuberant growth as with stunted specimens.

Area.	Specimens.	Decollated.	per cent.
A	426	16	3·8
B	408	8	2·0
C	750	6	0·8
D	989	9	0·9
E	421	0	0·0
Total	2,994	39	1·3

§9. *Summary.*—(1) *Clausilia bidentata* from small loci of similar character within a few yards of one another do not usually differ in size.

(2) *Cl. bidentata* and *Ena obscura* from different areas in the same wood 50 to 300 yards apart may definitely differ in size.

(3) The size variation in the two species runs parallel.

[1] The differences A/C, A/D, and A/E alone are significant.